Out of Africa—the Origins of the Tapeworms

Tapeworms are among the most disgusting but intriguing parasites of humans and other animals. They occur worldwide, causing malnutrition, sickness, and occasionally the death of their hosts. Yet, despite their economic significance, little has been known about how and when these parasites first attacked humans.

Now, ARS zoologist Eric P. Hoberg, who is in the Biosystematics Unit of the Parasite Biology, Epidemiology, and Systematics Laboratory at Beltsville, Maryland, has made a remarkable discovery—one that contradicts long-held theories.

"Traditionally, scientists believed that about 10,000 years ago—coincidental with the domestication of intermediate hosts such as cattle, swine, and companion carnivores like dogs—three species of taeniid tapeworms became associated with humans," Hoberg says.

But he and colleagues Alan de Queiroz and Nancy L. Alkire at the University of Colorado-Boulder and Arlene Jones at The Natural History Museum in London have uncovered new genealogical evidence that contradicts the traditional theory that humans got these parasites from domesticated animals. Their work is based on comparative morphology and DNA sequence analyses of parasites.

By studying the present-day ecology and geographic distribution of these parasites and their hosts, the researchers have uncovered new information about a long ancestry reflecting millions of years of host associations.

Hoberg curates the U.S. National Parasite Collection at Beltsville. It is one of the world's largest collections of parasites of humans and animals—containing several million specimens. One of his roles as curator is as a systematist—that is, discovering, describing, and developing concepts for the evolution and biodiversity of parasites.

"Pathogenic macroparasites, like tapeworms, have parasitized the world's vertebrates and invertebrates for millions of years," says Hoberg. "And although they remain a constant threat to economically important fisheries, livestock, and wildlife, only about one-third have been described or named.

"Our incomplete knowledge and understanding of taxonomy and species-level relationships of these parasites has hindered our full understanding of their host associations—final and intermediate—and their potential for causing disease," says Hoberg.

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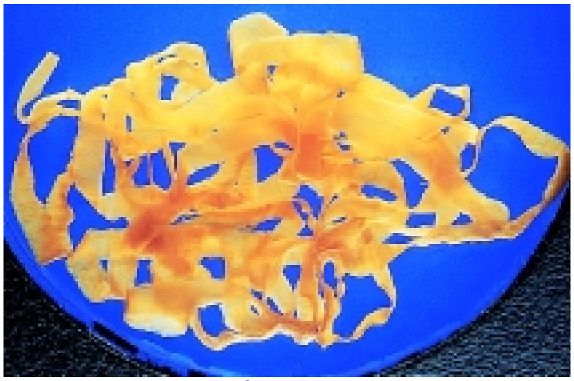

Adult specimen of the pork tapeworm, *Taenia solium*, from the intestine of a human.

The disease caused by tapeworms is known as cestodiasis. As a systematist, Hoberg carefully examines living species of tapeworms and other parasites and describes them by meticulously detailing their distinguishing characteristics—morphological, biochemical, and molecular. (See "Searching for Parasitic 'Roots,'" *Agricultural Research,* December 1996, pp. 4-7.)

"Systematists deal with taxonomy, phylogeny—that is, recognizing evolutionary relationships among species—and ultimately, classification, in which organisms are grouped hierarchically based on their evolutionary relationships," says Hoberg. "These classifications represent everything we know about the relationships among these organisms.

"More importantly," he says, "these classifications help predict species behavior. If we know which order, family, or genus a parasite is in, we can predict—with some certainty—patterns of life history and what effect it will have on hosts within the same or related families.

"Parasites have characteristic host and geographic distribution, as well as predictable life cycles and transmission patterns," says Hoberg. He's one of just a few U.S. systematic parasitologists who also examine where parasites are distributed geographically and how they coevolve with their hosts.

Looking at Clues From the Past

Hoberg uses the vast U.S. National Parasite Collection and his expertise in parasite systematics to examine evolutionary relationships between hosts and parasites. This research, called cospeciation analysis, includes studies of where hosts and parasites occur now and where they originated.

"The past is the key to the present," Hoberg says. "Historical studies involving tapeworms contribute to a predictive foundation for understanding today's environments and communities of living things. Besides telling us something about their hosts, parasites can tell us about their geographical links to long ago. They're both the products of a current environment and, at the same time, of a long ancestry reflecting millions of years of association with their hosts."

Hoberg's past research includes studies of the systematics and evolution of tapeworms of seabirds, seals, and sea lions. This expertise has helped him to examine tapeworm cospeciation and to perform biogeographic analysis—the study of their geographic distribution.

Based on their analysis, Hoberg's team showed that 12 named genera of taeniid tapeworms belong to 1 genus, *Taenia.* Recently, they completed the first phylogenetic study of *Taenia* species based on analyses of morphological

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Specimens and information databases of the U.S. National Parasite Collection are a unique and irreplaceable resource for parasite biodiversity research. Zoologist Eric Hoberg examines a specimen.

characteristics of adult and larval parasites. Their study "provides information that will enhance our ability to predict and understand the life history and geographic distribution for this large genus," Hoberg says.

Basic Life Cycle of the Parasite

"Taenia tapeworms can range in size from about 0.04 inch to over 50 feet," says Hoberg. "They're internal parasites, infecting all types of mammals—including humans and domestic animals. Their life cycles are very complex. They require one intermediate host—always an herbivore—and a final or definitive host—always a carnivore— in which to reproduce." The final host is the host in which the adult tapeworm lives.

Taeniid tapeworms have a global economic impact because of the sickness and death they can cause in humans and the production losses in domestic stock, including cattle and swine. Hoberg says, "Three species of these taeniid worms—*T. solium, T. saginata, and T. asiatica*—infect only humans. Their life cycles depend on domesticated cattle and swine as intermediate hosts."

The pork tapeworm, *T. solium*—often found wherever raw or undercooked pork is eaten—lives in the human intestine in its adult stage. Each segment, or proglottid, may contain as many as 40,000 eggs.

"Like most tapeworms, *T. solium* are hermaphroditic. That means that functional reproductive organs of both sexes occur in the same individual," Hoberg says, "and they're often self-fertilizing."

If the embryos, which pass out with the host's feces, are then eaten by a pig, the larvae emerge in the pig's digestive tract. They bore through the intestinal wall into a blood vessel and are carried to muscle tissue where they encyst, or form a protective capsule. The larval parasite that develops is then called a cysticercus, or bladder worm.

"If the cysticercus is eaten alive in raw or undercooked meat or a visceral organ like the liver, it attaches itself to the final host's intestine and develops directly into a mature adult," Hoberg says. This completes the *T. solium* life cycle.

"*T. solium* is unique in having a broad range of intermediate hosts such as domestic and wild swine, dogs, and primates including humans. But only humans serve as final hosts," Hoberg says.

The life cycle of the beef tapeworm, *T. saginata,* which occurs worldwide where beef is eaten raw or improperly cooked, resembles that of the pork tapeworm. With this species, cattle serve as the intermediate host, while humans are the final host.

Humans Got Tapeworms First!

Hoberg and his colleagues have evidence—phylogenetic, geographic, ecological, and molecular—indicating that, well over 10,000 years ago, ancestors of modern humans, living on the savannas of Africa, became hosts for *Taenia.*

"This occurred before the origin of modern humans and substantially earlier than the domestication of swine and cattle and the development of agriculture," he says. This conclusion was inferred from an examination of evolutionary histories for hosts and parasites and from evidence for the rate of molecular evolution between *T. saginata* and *T. asiatica.*

About 2 million years ago, Hoberg believes, African hominids (our early ancestors), who scavenged for food or preyed on antelope and other bovids, were exposed to colonization by these tapeworms. "The worms were using hyena and large cats as definitive hosts and bovids as intermediate hosts."

Hoberg says that species of *Taenia* tapeworms are historical ecological indicators of the foraging behavior and food habits of our early ancestors during the diversification of *Homo sapiens,* or humans. "These tapeworms tell a story about the ecological linkage between hominids and large carnivores that shared prey on the savannas of Africa."

Hoberg says, "Surprisingly, rather than humans' acquiring *Taenia* from cattle and pigs, we believe man gave tapeworms to these domestic animals, because the association between *Taenia* and hominids was established before the domestication of these food animals."

In fact, transmission from humans, he says, has occurred at least three times, represented by *T. saginata* in cattle and *T. asiatica* and *T. solium* in swine. "This means that the spread of *T. solium* among humans may have been enhanced by cannibalism or by humans eating dogs."

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Hoberg examines a specimen of a *Taenia* tapeworm from a North American lynx.

Hoberg's team did DNA studies that gave more evidence for the idea that prehumans acquired these tapeworms before cattle and swine were domesticated about 10,000 years ago. When the team studied the DNA of these worms, they estimated—based on a molecular clock—that divergence between the human-parasitic sister species *T. saginata* and *T. asiatica* occurred at least 160,000 years ago. "These sister species may have diverged coincidental with the migration of early humans from Africa to Asia," says Hoberg. "There, the worms continued to parasitize their hosts, and an isolated group evolved to become *T. asiatica.*"

Hoberg's team's research provides new information for understanding the association between taeniid tapeworms and humans. It indicates that these parasites' origins are not linked to the "recent" domestication of food animals.

This discovery can also serve as collateral evidence for understanding the ecological setting for human evolution that can now be applied to detailed historical and anthropological studies.—By **Hank Becker,** ARS.

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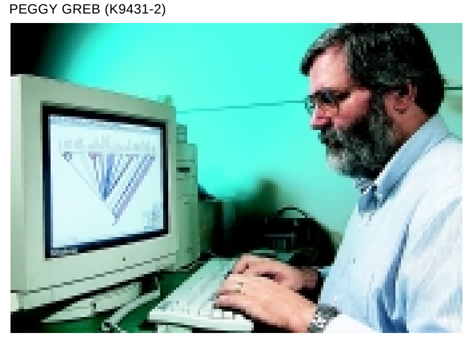

Hoberg reviews phylogenetic trees with information about carnivorous final hosts, herbivorous intermediate hosts, and geographic distribution.